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Taxodium distichum and related Species, with Notes on some geological Factors influencing their Distribution

By Roland M. Harper

Observations on the genus *Taxodium* in the field during three or four seasons have led me to the conclusion that there are at least two well-marked species in the southeastern United States. Most authors who have written on the subject have considered the genus to be represented in that region by a single species, but some have admitted the existence of a variety in addition.

The genus was founded by L. C. Richard in 1810, with a single species, the *Cupressus disticha* of Linnaeus; and the number of living species in the world has since been variously regarded as from one to three, excluding species which are now referred to *Sequoia* and *Glyptostrobus*.

Before discussing the relationships of the two southeastern species it will be well to give their principal synonymy, which is as follows:

TAXODIUM DISTICHUM (L.) L. C. Richard, Ann. Mus. Par. **16**: 298. 1810

Cupressus disticha L. Sp. Pl. 1003. 1753. Type locality: "Virginia, Carolina."

Schubertia disticha Mirbel, Mem. Mus. Par. **13**: 75. 1825.

Taxodium imbricarium (Nutt.)

Cupressus disticha β imbricaria Nutt. Gen. **2**: 224. 1818.

Type locality: "From Florida to North Carolina, in swamps and ponds more remote from the sea."

Taxodium ascendens Brong. Ann. Sci. Nat. **30**: 182. 1833.

Type locality North American, but not specifically given.

T. distichum var. *imbricarium* Sarg. Sylva N. A. **10**: 152. 1896.

The latter form of the name was used by H. B. Croom in his Plants of New Bern (now Newbern), N. C., in 1837, by M. A. Curtis in his flora of North Carolina in 1867, and by Wood & McCarthy in their Wilmington (N. C.) Flora in 1886, but does not seem to have been properly published until it was taken up by Professor Sargent. Synonyms for these two species which are purely horticultural or of doubtful application are here omitted.

The principal objection to the recognition of the latter species as distinct seems to have been its supposed intergradation with *T. distichum.* Elliott,* writing a few years after Nuttall, says of *T. imbricarium:* "This is a small tree growing in pine-barren ponds. It produces its knobs (exostoses) more abundantly than the large variety; and on its lower branches the leaves are frequently imbricated after the manner of the junipers. But on the upper branches the leaves are often expanded and distichous. It is perhaps only a stunted variety, growing in an unfavorable soil."

Seventy-two years later Professor Sargent† remarks: "No one unfamiliar with the fact that branches of the two forms occasionally appear on the same individual would imagine that the cypress trees with erect or pendulous thread-like branches and closely appressed acerose leaves belong to the same species as those with spreading distichous branches and flat leaves."

Dr. Mohr's observations on *Taxodium* in his "Plant Life of Alabama"‡ are of interest as being among the latest published. On page 117, in speaking of the mesophile and paludial forests of the lower division of the coast pine belt, he says: "Groves of the pond or upland cypress just mentioned—a variety closely connected with the type by intermediate forms—cover the shallow pine-barren ponds and semi swampy woods of a poor, sandy soil destitute of vegetable mold. This form of the cypress in the size and quality of its wood is greatly inferior to the typical cypress of the alluvial swamps, and is at once recognized by the leaves, which are closely appressed to the deciduous annual shoots. By this peculiarity of the foliage a check to excessive transpiration is provided during the time of drought, when the sandy soil is laid bare to the sun and its supply of water is failing."

On page 325 he says of the same plant: "Of smaller size than the species, with the leaves reduced in size and closely adpressed to the deciduous branchlets, thus imparting to the tree a strikingly peculiar aspect. This character, however, is not constant, and the variety can scarcely be maintained, the same individual producing during the earliest stages of growth and on vigorous adventitious shoots leaves of the ordinary form. This form passes freely into the species where the soil conditions are more favorable."

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* Bot. S. C. & Ga. **2**: 643. 1824.

† Sylva N. A. **10**: 152. 1896.

‡ Contr. U. S. Nat. Herb. **6**: 1901.

But, notwithstanding the opinions of these eminent botanists, it seems to me that the intergradation is more apparent than real, and that this idea may have arisen from a too hasty generalization of observed facts. It is true that young shoots of *T. imbricarium* often bear branchlets with distichous leaves (perhaps indicating its descent from an ancestral form which resembled *T. distichum* of the present day), but on the typical *T. distichum* I have seen only one kind of branchlets.

The opinions of Nuttall and Croom, both of whom seem to have been very acute observers, are more favorable to my view of the distinctness of the two species under consideration.

Nuttall, in the original description of *T. imbricarium*, says: "Leaves subulate, partly imbricated in four ranks, deciduous; nuts larger, chestnut colored." * * * "A smaller tree than the preceding, often producing fruit at a height of three feet from the ground."

Croom, in his flora of Newbern above mentioned, says (page 48): "*Taxodium distichum.* * * * Elliott expresses the opinion that the variety *imbricarium* of Nuttall is only this species in a starved condition, as it is commonly found in pine-barren ponds. But in some instances (20 miles above New Bern) I have seen large trees of this variety, and, in one instance, I observed it growing by the side of the common variety, and in the same soil."

The differences between the two species will now be considered more in detail. These differences are of several kinds, not only structural but ecological as well.

The most conspicuous structural difference, as noted by most of the authors just quoted, is in the form and position of the leaves and the branchlets which bear them. In *T. distichum*, as is well known, the leaves are two-ranked on the branchlets, widely spreading, and in the same plane, making each leafy branchlet resemble a pinnate leaf (to which it is indeed analogous); and the branchlets spread approximately horizontally, bringing the surfaces of the leaves likewise into a horizontal position. In *T. imbricarium*, on the other hand, the leaves are normally more or less appressed to the branchlets, which have lost their dorsiventral character. The branchlets have been described by Professor Sargent and others as "erect or pendulous," and from a herbarium specimen it would usually be impossible to ascertain which of these two positions they had assumed in life. But they would be much more correctly described as normally erect, occasionally somewhat spreading, very rarely (never in perfect specimens) drooping. It is interesting to note that the leaves and branchlets of the two species of the allied genus *Sequoia* differ in much the same way.

I have not noticed any difference between the fruits of the two species, but Nuttall says of *T. imbricarium* "nuts larger," and Endlicher * probably following Nuttall, says of *T. ascendens* Brong., "seminibusque majoribus."

The difference in size, mentioned by some authors, does not appear to be constant, as remarked by Croom. In Georgia, where both species are abundant, *T. imbricarium* often attains as large a size as *T. distichum*, but the former probably begins to fruit at a smaller size (though perhaps not at an earlier age, as it is said to be of slower growth).

One characteristic difference, which does not seem to have been noted before, is found in the enlargement at the base of the trunk, which is usually more abrupt in *T. imbricarium* than in *T. distichum*. In Coffee county, Georgia, I have walked entirely around a specimen of *T. imbricarium* on its enlarged base, a feat which would be impossible with any specimen of *T. distichum* I have ever seen. Furthermore, the enlargement of the trunk of *T. distichum* is approximately conical, with its greatest slope at or below the surface of the ground (or water, as the case may be), while that of *T. imbricarium* is conoidal, with its greatest slope some distance (a few inches to a foot or two) above the ground. In the many thousands of individuals of *T. imbricarium* which I have seen I have never observed any deviation from this character. The longitudinal ridges traversing this enlargement are usually quite sharp and prominent in *T. distichum*, and rounded or almost wanting in *T. imbricarium.* The same differences are often observable in cultivated specimens.

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* Syn. Con. 69. 1847.

The general appearance of the trunk of *T. distichum* is well shown in figure 48 of Schimper's Pflanzengeographie, which is a full page half-tone reproduction of a photograph taken by Dr. H. J. Webber in Florida,* also by plate 8 and figure 30 of Professor N. S. Shaler's paper on the fresh-water morasses of the United States in the Tenth Annual Report of the U. S. Geological Survey, and by plate 73 in Mr. Kearney's recent paper on Dismal Swamp,† which is the same as Professor Shaler's plate 8.

Plate 68 of Mr. Kearney's paper illustrates very well the character which I have just assigned to *T. imbricarum,* and plate 9 of Professor Shaler's paper, which was evidently photographed at about the same time and place, shows the same thing, though less distinctly. By comparing these plates with the illustrations of *T. distichum* just cited, the difference is readily seen. Nothwithstanding the fact that this species is not mentioned by Mr. Kearney in his paper (and he has since told me that he is not acquainted with it), I am confident that his plate 68 and Professor Shaler's plate 9 represent the true *Taxodium imbricarium.* I find no other record of the occurrence of *T. imbricarium* in Virginia than these two illustrations, but Croom found it near Newbern, N. C., which is only about 100 miles from Lake Drummond, Virginia, where the photographs in question were taken.

Whether the knees afford any diagnostic characters or not I am unable to state at present. Elliott mentions those of *T. imbricarium* as being more abundant than those of *T. distichum,* but this may not be universally true. Professor Shaler (in the paper above cited) and perhaps other authors, have noted that *T. distichum* cannot live with its knees under water during the summer. This is probably not true of *T. imbricarium,* for I have seen it in midsummer in ponds and creeks where no knees were visible, at least at the ordinary stage of water. The knees of *T. imbricarium* probably never become so large as those of *T. distichum.*

Physical tests show an appreciable difference in the wood of the two species. Dr. Filibert Roth, in one of the publications of the U. S. Department of Agriculture,* although not regarding the two forms as specifically or even varietally distinct, has tabulated the results of many tests which show that the wood of the "pond-cypress" is both heavier and stronger than that of the better-known plant.

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* The same photograph is reproduced in Coulter's "Plant Relations," as Fig. 91.

† Contr. U. S. Nat. Herb. 5 : 321–550. *pl. 65–77. f. 51–90.* 6 N. 1901.

Turning now to ecological characters, the leaf-galls may be considered next. The leaves of both species are frequently more or less infested with galls, and as far as I have observed the galls on the two species appear to be different. Whether they are caused by the same or different insects I do not know; this is a matter which deserves further investigation.

In regard to habitat, it seems to be the prevailing opinion that *T. distichum* is confined to river swamps and *T. imbricarium* to pine-barren ponds. This, however, is not always the case. The largest specimens of *T. imbricarium* I have ever seen are in southeastern Georgia, in deep-flowing water of creeks which never dry up, and yet they maintain their essential characters perfectly. Here the species is to all outward appearances growing under practically the same conditions which prevail in the rivers and creeks which *T. distichum* inhabits. The habitat of the latter is also somewhat variable, including lime-sinks as well as river-swamps. Some say that *T. imbricarium* grows in poorer soil, but this also is liable to many exceptions, to say nothing of the difficulty of defining accurately what constitutes a poor soil.

In view of all these well-marked and constant differences, and others to be mentioned later, it seems to me that *Taxodium distichum* and *Taxodium imbricarium* can no longer be consistently treated otherwise than as distinct species. They are certainly as distinct as *Lycopodium lucidulum* and *L. porophilum*, *Juniperus Virginiana* and *J. Barbadensis*, *Pinus palustris* and *P. heterophylla*, and a hundred others which might be mentioned.

During my investigations of the flora of Georgia in 1900, I discovered a most remarkable relation between the habitats of these two species of *Taxodium* and the geological formations, on which I have based a new theory of their distribution. This theory has so far been fully substantiated by observed facts in almost every case, and the few apparent exceptions to it which have been noted will probably disappear on closer investigation. It may be briefly stated as follows:

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* Circ. Div. Forestry, 19: 22. 1898.

Taxodium imbricarium always grows over the Lafayette formation; Taxodium distichum never.

Furthermore, *T. imbricarium* seems to occur only on Lafayette which is overlaid by a thin deposit of the Columbia formation, and *T. distichum* is often, if not usually, found on the Columbia also, but where this formation is absent it may grow directly on the older strata.

The Lafayette and Columbia formations have been thoroughly discussed by W J McGee,* but a brief outline of them here may be of interest to those who have not time to read the one hundred and seventy-five quarto pages of his monograph.

The Lafayette, the older of the two, is (at least throughout most of the region in which *Taxodium imbricarium* occurs) a deposit of sandy clay, reddish or yellowish in color, varying considerably in thickness, lying unconformably on the mesozoic and cenozoic strata over a vast area of the coastal plain of the eastern United States. It is supposed to have been laid down just before the Glacial period of the North, during a submergence of the coastal plain estimated to have lasted about 60,000 years.

The Columbia formation, in the region under consideration, consists almost entirely of sand. It is supposed to have been deposited during a much shorter period of submergence of the coastal plain contemporaneous with or subsequent to the glacial period. It is always above the Lafayette where the two come in contact, and is rarely too thick for the roots of trees to penetrate through it into whatever strata may be beneath.

In a general way the terrane of the Lafayette may be said to coincide with the present coastal plain from Maryland to Texas, extending up the Mississippi Valley to Illinois, with the following exceptions. It is not known to cover any portion of Florida except the extreme north, the peninsula having perhaps been too far off shore during the Lafayette submergence to receive any of these sediments. Neither is this formation known to extend to the present shore line at any point.

During a period of elevation succeeding the Lafayette submergence the larger rivers of the coastal plain cut their channels entirely through the Lafayette deposits into the older strata below, and in most of the resulting gorges the Columbia sands were subsequently deposited.

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* Ann. Rep. U. S. Geol. Surv. 12^1: 347–521. *pl. 32–41. f. 28–72.* 1891.

Like the Lafayette, the Columbia covers a large part of the coastal plain, extending from Long Island to Mexico, and up the Mississippi and Ohio rivers to Indiana. In the Middle and South Atlantic States it covers the whole country near the coast, but usually does not extend up to the inland edge of the coastal plain like the Lafayette. In southwestern Georgia and Alabama, however, it is mostly confined to the river valleys, the divides here having been above the sea during the Columbia submergence. In Texas, while the main body of the Columbia only covers the seaward portion of the coastal plain, long narrow arms of this formation extend several hundred miles up the larger rivers, far beyond the inland edge of the costal plain. Similar extensions are found in Arkansas and the Indian Territory. On the peninsula of Florida the Columbia formation has not been traced south of latitude 28°.

The geographical distribution of our two species of *Taxodium* is intimately related to that of the two geological formations just mentioned, as will now be shown.

The range of *T. distichum* is given by Professor Sargent * as follows: "From southern Delaware * * * southward near the coast to the shores of Mosquito Inlet and Cape Romano, Florida, through the coast region of Gulf States to the valley of the Devil River in Texas, and through Louisiana and Arkansas to southeastern Missouri, eastern Mississippi and Tennessee, western and northwestern Kentucky, southern Illinois, and Knox county in southwestern Indiana."

The range thus given of course includes that of *T. imbricarium* also, but according to my theory *T. distichum* would be confined to the comparatively small but widely distributed area from which the Lafayette formation is absent, such as near the coast, along the larger rivers, and on the peninsula of Florida.

Among the extreme points of the range of *T. distichum* may be mentioned the following:

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* Sylva N. A. 10: 153. 1896.

Dr. Hollick* has reported its occurrence near Newark, N. J., but is not certain that it is indigenous there. This locality is near the extreme northern limit of the Columbia formation, and about 200 miles from any known area of the Lafayette. The occurrence of *T. distichum* at this point therefore does not conflict with my theory. The Lafayette formation is also unknown in Delaware, which is the northernmost state in which *T. distichum* is undoubtedly indigenous at the present time.

Dr. Gattinger, in his Flora of Tennessee (pages 25 and 32 of the 1901 edition), mentions its occurrence along the Tennessee River, which, according to Dr. McGee's map of the Lafayette and Columbia formations (plate 38 of his monograph above cited), has cut through the Lafayette and is now lined by deposits of Columbia throughout most of its course through the western part of the state.

Dr. Mohr† says of the range of *Taxodium distichum* in Alabama: "This tree is found throughout the State," but this statement is probably to be taken with some qualification. Among the particular localities mentioned by him is the Tennessee River; and although the Columbia formation is not known to extend up this river into Alabama, the *Taxodium* might well do so, as it is not necessarily confined to this formation.

The occurrence of *T. distichum* in Knox county, Indiana, has been discussed by John S. Wright.‡ In Garden and Forest (**3**: *7. f. 2*) for January 1, 1890, there is a good half-tone engraving of an Indiana cypress swamp.

An interesting station for *T. distichum* in Texas was discovered in 1894 by Mr. A. A. Heller, who collected it along the Guadalupe River at Kerrville, at 1600 feet altitude.§ One of his specimens from this locality is in the Columbia University herbarium. Kerrville is beyond the known area of the Columbia formation, but it is noteworthy in this connection that this formation extends farther inland and higher above sea level along the rivers of Texas than anywhere else. According to Mr. Heller's report, Kerrville is "situated in a limestone formation." On investigation I find that this formation is lower Cretaceous. Professor W. L. Bray, of the University of Texas, to whom I wrote for further information about the range of *T. distichum* in that state, informs me that it occurs on almost every stream in the Cretaceous area of Texas and probably on all on the Rio Grande Plain, also in all the bayou country of east Texas, north to the Indian Territory line. Dr. Havard, in his "Report on the Flora of Western and Southern Texas," * mentions several stations for this species in the extreme southern part of the state.

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* Ann. Rep. State Geol. N. J. 1899: 181. 1900.

† Contr. U. S. Nat. Herb. **6**: 46. 1901.

‡ Proc. Ind. Acad. Sci. 1897: 172–175. 1898.

§ *Cf.* Contr. Herb. F. & M. Coll. 1: 9. 1895.

The southeastern limit of *T. distichum* has been placed by Professor Sargent at Mosquito Inlet (about lat. 29°) on the east coast and at Cape Romano (about lat. 26°) on the west coast of Florida, but Dr. Small, who has recently been in southern Florida, tells me that it extends down the east coast to Miami (which is farther south than either locality mentioned by Professor Sargent) and is common in the Everglades near by. This is considerably beyond the known area of the Columbia formation, but still farther from the Lafayette.

In Georgia, to which state my field work on this genus has been confined, I have seen *T. distichum* on the Oconee River in Montgomery county, on the Ocmulgee in Dodge and Wilcox, on the Flint in Sumter, Dooly, Dougherty and Decatur, on the Ochlocknee in Thomas, on the Chattahoochee River and Sowhatchee Creek in Early, on Lime Creek in Sumter and Gum Creek in Dooly, on Muckalee Creek in Lee and Kinchafoonee in Lee and Terrell, on Spring Creek in Decatur, Ichawaynochaway in Calhoun and Chickasawhatchee in Dougherty; from all of which points the Lafayette formation is known or believed to be absent. I have also observed this species in a few scattered localities away from the rivers in Sumter, Lee and Dougherty counties (from which localities the Lafayette may be inferred to be absent, though we have as yet no direct evidence that such is the case), and in lime-sinks near the Flint River in Dooly county. Other botanists have collected or observed it along the Savannah and Altamaha rivers; and it doubtless extends from all the points just mentioned down each river nearly or quite to its mouth.

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* Proc. U. S. Nat. Mus. 8: 504. 28 S. 1885.

The range of *T. imbricarium* is not so well known, as comparatively little attention has been paid to this species. Although it appears to be much more abundant than *T. distichum* in most of the states in which it grows, most botanists who have observed it have probably considered it identical with that species, and therefore made no especial note of it. It is not even mentioned in any edition of Chapman's "Flora of the Southern United States."

Professor Sargent * says of the range of this species: "The acerose form * * * is not uncommon in South Carolina, in northern Florida, and in the neighborhood of Mobile, Alabama." It has also been reported from North Carolina by Nuttall, Croom and others, and is very abundant in Georgia, where it perhaps reaches its best development. The evidence in favor of its occurrence in Virginia has already been given. Outside of these six states I find no record of it.

T. imbricarium is common wherever the conditions of soil and topography are favorable for its development, in those portions of the coastal plain where both the Lafayette and Columbia formations are present, away from the coast and larger rivers. It seems to approach nearest to the coast in North Carolina, where Wood and McCarthy have recorded a station for it in their Wilmington Flora,† in a swamp about six miles from the ocean, in New Hanover county. In Chatham county, Georgia, I noticed last June that it extended to within twelve miles of Savannah on both the Central of Georgia and Georgia and Alabama Railways. These two railroads run almost perfectly straight through the county, and at the points mentioned they are about a mile apart. On consulting Mr. McGee's map I found that these localities are just at the coastward edge of the Lafayette formation, thus furnishing additional evidence in support of my theory.

Of the inland limit of *T. imbricarium* little is known. In the eastern part of Georgia I have seen a few specimens as far up as Millen, 78 miles from Savannah, and in the western part it is abundant in certain spots as far up as the southeastern corner of Sumter county, 200 feet above sea-level, 180 miles west of Savannah and about 125 miles north of the Gulf of Mexico. Here it extends to the inland edge of the Oligocene strata. Croom * has reported it from Hartford, Ga. (a settlement, now extinct, which was near the Ocmulgee River in Pulaski county, about opposite the site of the modern town of Hawkinsville), which is about the same distance from the Atlantic coast as that last mentioned.

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* Sylva N. A. **10**: 152, in footnote.

† Jour. Elisha Mitchell Sci. Soc. **3**: 123. 1886.

Between these limits *T. imbricarium* is very abundant in Georgia; and I will here give its observed distribution in the state somewhat in detail, as it is on these observations that my theory of its distribution is chiefly based.

East of the Ogeechee River it is abundant in the wet pine-barrens of Chatham and Effingham counties, and is sparingly represented around Millen, in the southern corner of Burke. West of the Ogeechee, in Emanuel and the upper part of Bulloch, I have seen it only in creeks and small rivers, where, as before mentioned, it attains a considerable size. Traveling westward along the Georgia and Alabama Ry., I saw it last July at many points in the pine barrens of Tattnall, Telfair, Dodge, Wilcox and Dooly counties, extending to within eight or ten miles of Cordele. Between Cordele and the Flint River the Columbia formation seems to be absent, and *Taxodium imbricarium* likewise. Farther south it occurs in wet pine-barrens or in small sluggish pine-barren streams in Worth, Berrien, Coffee, Ware and Appling counties. In the upper part of Coffee county, as for instance in the vicinity of Douglas, it grows also in creeks as in Bulloch.

In Sumter it seems to be confined to a number of shallow ponds about three miles from the Flint River in the southeastern corner of the county, where the Lafayette and Columbia formations overlap a short distance. Southward from there, it is very abundant in Lee county, and occurs in Dougherty, Calhoun, Mitchell, Miller, Early, and the northern parts of Thomas and Decatur, in the terrane of the Lower Oligocene. Throughout this part of the state its usual habitat is in shallow pine-barren ponds which sometimes dry up in summer, which it occupies to the exclusion of other trees. But in Thomas and Decatur counties (east of the Flint River) I have seen it in permanent ponds several hundred acres in extent and probably five or six feet deep, containing a luxuriant growth of various Nymphaeaceae and other strictly aquatic plants.

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* Am. Jour. Sci. **28**: 166. 1835.

At every point where *Taxodium imbricarium* has been observed all the indications are that both the Lafayette and Columbia formations are present, though of course I have been able to actually verify this only in comparatively few cases.

The cause of the preference of these two species of *Taxodium* for different superficial formations is as yet unknown, but the comparative imperviousness of the Lafayette clays doubtless has something to do with it.

If my theory is absolutely correct, these two species would never be found together. One or two exceptions to this have been noted. On July 13, 1901, I found both species together in a swamp in the pine-barrens in the northeastern part of Lee county, Georgia. But it is noteworthy that the specimens of *T. distichum* appeared stunted and unhealthy, while those of *T. imbricarium* were of the usual size and appearance. One explanation of their occurrence together might be that the seeds of *T. distichum* had been brought there in some manner and that the trees had managed to grow in spite of the unfavorable environment. I did not notice any fruit on these specimens of *T. distichum*, and the species is perhaps not reproducing itself at this locality. A similar or analogous state of affairs may prevail at the locality in North Carolina mentioned above, where Mr. Croom observed both species growing together.

It might be remarked here that there has been some difference of opinion among geologists as to whether the Lafayette formation extends beneath the Okefinokee Swamp in southeastern Georgia. If my theory is true this question could easily be settled by a determination of the species of *Taxodium* inhabiting the swamp. So far as I know no botanist has yet penetrated this vast swamp, but there can be no doubt that it contains at least one of the species of *Taxodium*, for cypress timber is said to be one of its principal resources, and the chief cause of the destruction of the swamp which is unfortunately now in progress.

In addition to the influence of the Lafayette and Columbia formations on the distribution of these two species, the older underlying strata also seem to have a considerable influence. For instance, both species seem to grow only over calcareous substrata. *T. distichum* is almost entirely restricted to the Cretaceous and later formations of the coastal plain, but if Dr. Mohr's report of its occurrence on the Tennessee River in Alabama is correct, it there extends beyond the inner edge of the coastal plain into the Palaeozoic region. In Georgia it does not seem to extend even as far inland as the Cretaceous, but probably neither the topography nor the chemical composition of the rocks in the Cretaceous region of Georgia are adapted to either species of *Taxodium*, for the country is quite hilly, with few swamps or ponds, and the rocks are mostly argillaceous.

The habitat of *T. imbricarium*, so far as underlying formations are concerned, seems to be still more restricted than that of *T. distichum*. I do not know of its occurrence on strata older than Tertiary, and it may not extend farther inland than the Oligocene division of the Tertiary.

The difference between *T. distichum* and *T. imbricarium* may be of comparatively ancient origin, for fossils resembling both species are found in the Cretaceous and Tertiary strata of North America and Europe. Some of the fossil species of *Taxodium* with spreading leaves are referred to our living species *T. distichum*, but those with appressed leaves are usually referred to the related genus *Glyptostrobus*, which seems to be represented among living plants only by a single Asiatic species. More will be said of this genus later.

But if both of our species of *Taxodium* have existed since Cretaceous times, the question will naturally arise, what were their respective habitats before the Lafayette period, and also during that period, when the present coastal plain was all submerged? I am not prepared to answer this question completely, but would suggest as a partial solution that *T. imbricarium* has been evolved from the ancestors of *T. distichum* since the Lafayette period, and for this reason the two species are not yet as completely differentiated as are those of more ancient origin. The occurrence of distichous spreading leaves on the branchlets of the young shoots of *T. imbricarium* would seem to substantiate this view, for young shoots are usually supposed to show ancestral characters.

It seems to be a well-established fact that *T. distichum* grew as far north as Greenland in Miocene times. With the advance of the ice-sheet during the Glacial period it was probably driven southward into Mexico, where the same species or a closely related one exists to-day. In the meanwhile the deposition of the Lafayette formation had taken place, and with the retreat of the ice our *Taxodium* doubtless migrated northward and eastward until it occupied its present territory. It was probably during this migration over the newly deposited Lafayette that the differentiation into two species took place, and *T. imbricarium* was evolved.

Some of the authors quoted at the beginning of this paper have mentioned the occurrence of forms intermediate between *T. distichum* and *T. imbricarium*. These might be of two kinds: first, individuals bearing branchlets of both kinds, and second, individuals all of whose leaves are intermediate in form and position.

The first case has been already discussed, and seems to present no difficulty. Individuals of the second kind also exist, and may perhaps even represent a distinct species. Such an intermediate form is probably what Brongniart [*] described as *Taxodium microphyllum*, and Parlatore [†] as *T. distichum β microphyllum*, so that names are not lacking for it. The only locality cited by Parlatore for his variety is Louisiana, while the typical *T. imbricarium* is not known west of Alabama. This may be an indication of the progressive differentiation of the species as the genus migrated eastward along the Gulf coast after the Glacial period.

In Georgia I have seen this intermediate form only in and near the Ogeechee River, at Millen, Ogeechee, Rocky Ford and Meldrim. What the relations of the Lafayette and Columbia formations are at these points I have not yet determined.

There is another supposed species of *Taxodium* in Mexico, *T. mucronatum* Tenore, of which comparatively little is known. Most of the accessible information about it has been summed up by Professor Sargent, [‡] who is inclined to believe that "it may prove to be a mere geographical form of our tree." Professor Bray, in writing to me of the range of *T. distichum* in Texas, expresses the opinion that this species as it passes into Mexico becomes "Sonorized," as several other species do, and is another thing. It is possible that *T. distichum* intergrades with *T. mucronatum* as suggested by Professor Bray. The two species are scarcely distinguishable in the herbarium, the characters by which they are separated being mostly phaenological. Mr. Heller's specimens from Kerrville, Texas, seem to resemble the latter as much as they do the former, at least in their visible structural characters.

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[*] Ann. Sci. Nat. 36 : 182. 1833.

[†] DC. Prodr. 16 : 441. 1868.

[‡] Sylva N. A. 10 : 150. 1896. Gard. & For. 10 : 451. July 17, 1897.

One other point now remains to be considered, namely, the relation between *Taxodium* and *Glyptostrobus*. The latter genus was founded by Endlicher (Syn. Con. 69) in 1847, with two species, *G. heterophyllus* and *G. pendulus*, said to be natives of China. (He enumerates also in the same work three species of *Taxodium*.) In 1880 this genus was united with *Taxodium* by Bentham and Hooker (Gen. Pl. **3**: 429). Eichler, in his treatment of the Coniferae in Engler and Prantl's Natürlichen Pflanzenfamilien, keeps the two genera apart, but considers the reasons for so doing scarcely sufficient. This subject has recently been more fully discussed by Dr. M. T. Masters,* who gives very good reasons for considering the two genera distinct. I have seen only one specimen of *Glyptostrobus* (*G. heterophyllus*, in the Columbia University herbarium) myself, but its appearance suggests that its leafy branchlets might not fall off with the leaves as in the case of *Taxodium*. This point is not mentioned by the authors just cited, and I have no means of verifying it at present.

But the question of the identity of *Taxodium* and *Glyptostrobus* is not of such immediate interest to us as the relation of *Taxodium imbricarium* to *Glyptostrobus pendulus*. These were both mentioned by Endlicher in his Synopsis Coniferarum who seems to have had no suspicion of their similarity, but they have been regarded as identical by some authors, and this is probably the case. Professor Sargent treats them as identical in his Sylva of North America (**10**: 152. 1896), and in Garden and Forest (**10**: 451) for July 17, 1897, writes as follows: "The tree which in the United States and Europe is almost universally called *Glyptostrobus pendulus*, is really a juvenile [*sic*] form of the *Taxodium* of the Southern States, *Glyptostrobus* being a south China genus

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*Jour. of Bot. **38**: 37–40. Feb. 1900.

with a single species, which has possibly never been brought to the United States, and which would not be hardy in this part of the country" [Massachusetts]. "It is a comparatively small tree in its native swamps, and, in spite of its southern home, is hardy in New England, where it is one of the most distinct and beautiful of the pyramidal conifers. The proper name for this tree is *Taxodium distichum*, var. *imbricarium*."

In front of the main building of the Department of Agriculture in Washington there are two trees of this species one labeled "Chinese Water Pine, *Glyptostrobus pendulus*, China," and the other the same except that it is called *G. Sinensis*. Scattered about the parks of the city are many similar specimens, as well as some of *Taxodium distichum*. Although they are rather pyramidal in shape, unlike *Taxodium imbricarium* in its native habitat, they have the appressed leaves and erect branchlets of that species, and seem to differ only in their peculiar shape, which is probably only the result of long cultivation under unnatural conditions. The only specimen of "*Glyptostrobus pendulus*" in the Columbia University Herbarium is from a tree cultivated in Philadelphia, and on the back of the sheet is written a note to the effect that it came from a seedling of *Taxodium distichum*.

In the Gardener's Chronicle (III. **26**: 489. *f. 161*) for December 30, 1899, there is a figure of one of these cultivated specimens growing in England, and it is there contrasted with *Glyptostrobus heterophyllus*, its identity with *G. pendulus* evidently being taken for granted.

The question might now arise: Are there really two species of *Glyptostrobus* in Asia? Apparently not; for no flora of China or Japan to which I have had access contains any reference to *G. pendulus*, and it is most likely that Endlicher described this species from a cultivated specimen, and erred in crediting it to China. A number of horticultural names which have been given to this cultivated plant may be found in Sargent's Sylva, among the synonyms of *Taxodium imbricarium*.

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